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Environmental controls and anthropogenic impacts on deep-sea sponge grounds in the Faroe-Shetland Channel, NE Atlantic: the importance of considering spatial scale to distinguish drivers of change

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Determining the scale of anthropogenic impacts is critical in order to understand ecosystem effects of human activities, within the context of changes caused by natural environmental variability. We applied spatial eigenfunction analysis to disentangle effects of anthropogenic drivers from environmental factors on species assembly in the Faroe-Shetland Channel (FSC), in the northeast Atlantic. We found that the species assembly considered here was structured at both small and large spatial scales. Specifically, substrate types, distance to oil wells and pipelines, the presence of objects and demersal fishing (both static and mobile) appeared significant in explaining large spatial scale species assembly structures. Conversely, temperature and variance in temperature shaped the species community across smaller spatial scales. Mobile scavenger species were found in areas impacted by demersal fishing. Oil and gas structures seemed to provide a habitat for a range of species including the commercially important fishes *Molva* sp. and *Sebastes* sp. These results demonstrate how the benthic ecosystem in the FSC has been shaped by multiple human activities, at both small and large spatial scales. Only by sampling datasets covering several sites, like in this study, can the effects of anthropogenic activities be separated from natural environmental controls.

Keywords: anthropogenic impacts, deep-sea sponge grounds, Faroe-Shetland Channel, fisheries, megafauna, oil and gas, spatial scale, species assembly

Introduction

Ecological communities and processes such as recruitment or dispersal vary over temporal and spatial scales (Wiens, 1989). Understanding appropriate scales for observing ecological processes, as well as determining the origin of spatial variation (biological, environmental, or anthropogenic), is very important to determine how ecosystems and communities function (Borcard *et al.*, 2018). Changing sampling scale when analysing the same ecological assemblage can lead to drastically different findings (Nogués-Bravo *et al.*, 2008) and spatial analysis has been increasingly used in ecology in recent decades (Dale and Fortin, 2014). This is particularly important with recent fast temporal changes observed in ecosystems as a consequence of human activities and global climatic change (Halpern *et al.*, 2008).

Determining spatial structure in complex ecological community datasets is challenging but a range of methods have been developed. Distance-based Moran's eigenvectors mapping or dbMEM is one method that can be applied to determine spatial structures in the composition of ecological communities (Borcard and Legendre, 2002). It creates new variables or eigenfunctions that correspond to the spatial scales perceivable in the community composition (Borcard *et al.*, 2004). Initially called Principal Coordinates of Neighbour Matrices (PCNM), dbMEM provides eigenfunctions calculated solely on geographical coordinates and pairwise distances between sampling points (Borcard and Legendre, 2002). After extraction of positive eigenfunctions maximizing Moran's index of spatial autocorrelation (Moran's I), dbMEM can help distinguish between spatial changes owing to community processes and spatial changes resulting from variations in environmental factors (Dray *et al.*, 2006). dbMEM analysis is a powerful tool for ecologists trying to understand the importance of spatial scales and can be combined with ordination analysis (Dray *et al.*, 2006) such as Principal Component Analysis (PCA) and Redundancy Analysis (RDA) (Henry *et al.*, 2013).

Deep-sea sponge grounds are present in many of the world's ocean and are constituted by high densities of one or more sponge species (Maldonado *et al.*, 2017). Sponge grounds provide a three-dimensional habitat known to support a great diversity of organisms, but also constitute a substrate that other organisms can colonize (Buhl-Mortensen *et al.*, 2010). Deep-sea sponge grounds have thus been shown to be associated with higher megafauna diversity and abundance compared with non-sponge habitats (Beazley *et al.*, 2013, 2015). When considered as a substrate, sponges themselves support higher species richness, biomass, and diversity than other hard substrates found in the deep sea such as coral rubble (Kazanidis *et al.*, 2016). Sponge spicule mats are additionally an important substrate type in the deep sea, supporting higher species diversity (Bett and Rice, 1992; Beaulieu, 2001; Laguionie-Marchais *et al.*, 2015). Sponge aggregations are also known to serve as nursery grounds for numerous vertebrate and invertebrate marine species, including economically-important fish (Okutani and Sasaki, 2007; Marliave *et al.*, 2009; Kenchington *et al.*, 2013).

In the Faroe-Shetland Channel (FSC) sponge grounds occurring at depths of around 500 m (Kazanidis *et al.*, 2019), are of the boreal ostur type formed by accumulations of demosponges, particularly *Geodia spp* (Bett, 2001; Klitgaard and Tendal, 2004). In July 2014, a United Kingdom nature conservation marine protected area (NCMPA) was established in the FSC to protect deep-sea sponge grounds. Nevertheless, fishing activities including trawling have been recorded within the FSC prior to the NCMPA designation (Bullough *et al.*, 1998). Oil exploration and production activities are also taking place in the FSC, within and around the NCMPA, since the early 1990s with the initial discovery of the Foinaven, Schiehallion and Loyal fields (Austin *et al.*, 2014) and the continued development of the Quad 204 project (Rees and Parke, 2013).

Most studies on deep-sea ecosystems consider the impacts from individual human activities at local sites. However, studies considering multiple anthropogenic activities over larger spatial scales are needed to better understand their impacts on deep-sea benthic communities, including sponge grounds. Here, we used seabed still images and environmental data from a range of academic and industrial sources to conduct a community-level spatial analysis of sponges and associated megafauna in the FSC. The objectives of this study were to: (i) untangle the impacts of environmental and anthropogenic factors on the distribution of megafauna including sponges in the FSC and (ii) determine at which spatial scales these environmental and anthropogenic factors influence local megafauna communities.

Material and methods

Sampling area

Still images from environmental monitoring surveys conducted at six sites within the FSC between 2002 and 2014 were accessed for this study: Clair, Foinaven-Schiehallion-Loyal, Laggan, Rosebank (along a proposed pipeline route), Suilven and William (Figure 1, Table 1). The FSC is located between the Scottish and Faroese continental shelves. To the southwest, the FSC reaches depths of about 850 m and is separated from the North Atlantic Ocean by the Wyville-Thomson ridge. To the northeast the FSC is open to the Norwegian Sea and deepens to almost 2000 m (Buhl-Mortensen, *et al.* 2010). In total, 4665 still images from ROV transects were catalogued and 2436 still images were selected for further analysis (Figure 1, Table 1). As images originated from 16 different surveys (Table 1), image selection was strict to only include images of the best quality. Images partly obstructed by sediments, too far away from- or too close to the seabed (below 1 m or beyond 2 m to the seabed), and images of poor resolution (less than 300 dpi) were not included in the analysis. Furthermore, since each survey covered different spatial areas, site will not be considered in this study as a variable but rather be used as parameter determining the origin of each still image.

Image analysis

For each still image, all clearly visible megafauna were recorded and classified into operational taxonomical units (OTUs). In total, 52 non-sponge OTUs were considered in the analysis (Table 2). As sponge identification requires biological samples and examination of their spicules, sponge OTUs were based on morphology alone based on definitions given in the literature (Boury-Esnault and Rützler, 1997) and a sponge catalogue developed for the FSC in Kazanidis *et al.* (2019). Hence erect sponge OTUs were grouped into the following six morphological groups: arborescent, i.e. branching, clathrate, i.e. lattice-forming, flabellate, i.e. fan-shaped, globular, massive, and carnivorous morphotypes (Table 2, Supplementary Figure S1). Three other sponge OTUs were defined to group the verrucose sponges, encrusting sponges, and cushion-shaped sponges respectively (Table 2; Supplementary Figure S1).

Dominant substrate type was also determined for each still image. Substrate types were categorised into the following five groups: (i) sand, (ii) cobble/gravel, (iii) sand with boulder, (iv) cobble/gravel with boulder, and (v) boulder, adapted from the Wentworth scale (1992). Finally, presence of oil and gas related objects and trawl marks as identified by Roberts et al. (2000) as distinctive linear scars on the seabed was recorded on each image (Figure 2).

Environmental and anthropogenic factors

In order to assess the importance of environmental and anthropogenic variables on the distribution of benthic megafauna in the FSC, data from several online resources were accessed. Slope, aspect, and rugosity were extracted from bathymetry shapefile available at the GEneral Bathymetry Charts of the Oceans (GEBCO; https://www.gebco.net, spatial resolution 30 arc second), using the freely available software QGIS (QGIS Development Team,

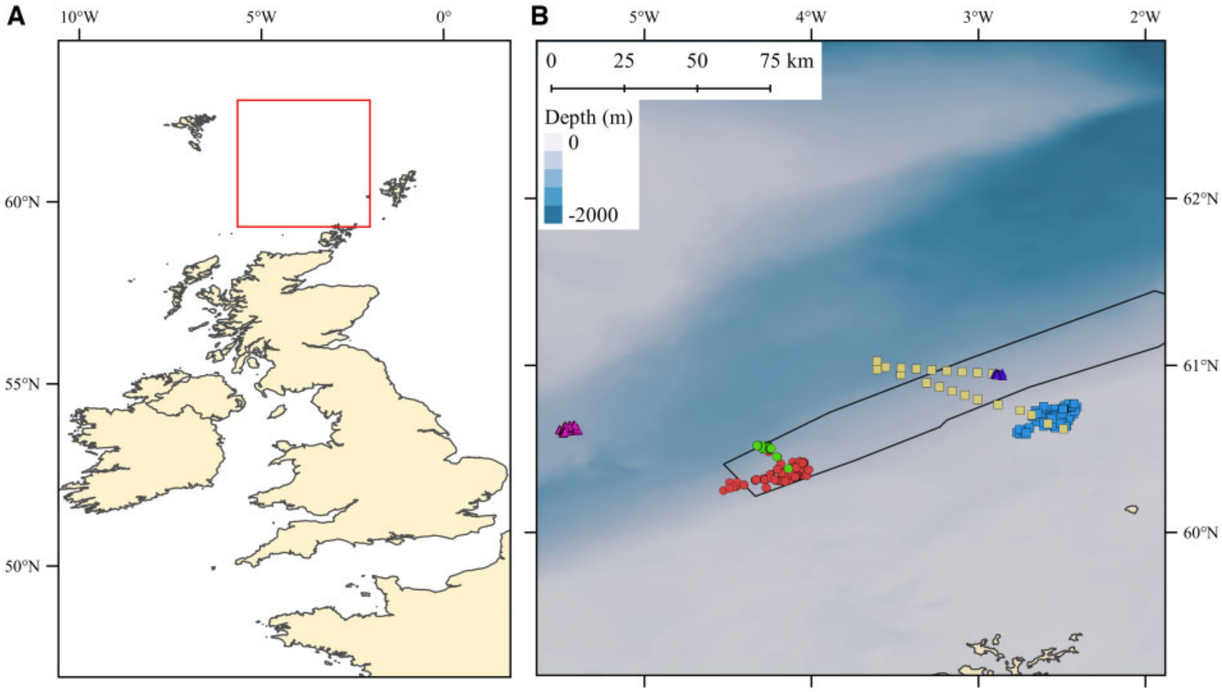

Figure 1. Location of the study area and of the still images analysed. (a) Location of the FSC highlighted in red. (b) Faroe-Shetland Channel NCMPA (outlined in black) with still images used in this analysis coloured by oil field (red - Foinaven-Schiehallion-Loyal, blue - Clair, purple - Laggan, yellow - Rosebank, green - Suilven and pink - William).

Table 1. Summary of still images processed.

Field	Location (Latitude, Longitude in DD)	Depth (m)	Numbers of surveys included in the analysis	Year of survey(s)	Number of images available	Number of images retained in the analysis
Clair	60.70, −2.51	123–176	4	2000, 2004, 2010, 2013	920	470
Foinaven-Schiehallion-Loyal	60.36, −4.09	361–925	8	2002, 2003, 2005, 2006, 2007, 2011, 2015, 2016	1525	935
Laggan	60.95, −2.87	567–601	1	2007	1322	490
Rosebank	60.94, −2.92	129–1118	1	2011	115	78
Suilven	60.51, −4.28	455–879	1	2002	181	66
William	60.63, −5.45	749–800	1	2006	601	397

2019). Aspect was subsequently converted into northness and eastness, as follows:

$$Eastness = \sin(Aspect), \quad (1)$$

$$Northness = \cos(Aspect). \quad (2)$$

Average annual temperature and salinity, variance of annual temperature and salinity as well as neap and spring seabed stress (parameters determining seabed disturbance arising from tidal currents) were available through the Atlantic Interactive project (unpublished data). Spring and neap estimates of bed stress were estimated from the NEMO simulation AMM60 with a 1.8 km resolution for the domain 40.1–64.9 DD latitude, and 24.9–17.3 DD longitude (Guihou and Polton, 2015; Guihou *et al.*, 2018). Surface and bed temperature and salinity data from 2000 to 2009 were modelled from a POLCOMS Atlantic Margin Model with ~12 km resolution and domain 40.1–64.9 DD latitude and 13.0–19.8 DD longitude (available at https://www.bodc.ac.uk/data/documents/nodb/316641/) (Holt *et al.*, 2012).

Static and mobile demersal fishing intensity (spatial resolution 0.01° by 0.01°) based on the vessel monitoring system (VMS) was acquired through the Marine Scotland Open Data Network Initiative National Marine Plan Interactive (NMPI, https://marinescotland.atkinsgeospatial.com/nmpi/). VMS data for UK registered commercial fishing vessels greater than 15 m long for the period 2009–2013 were combined with ICES landings to produce this layer (NMPI website). Distance to the closest well and distance to the closest pipeline were also calculated for each still image with the R package Geosphere (Hijmans, 2017) from Oil and Gas UK shapefiles available for visualization on the NMPI website.

Although most environmental and anthropogenic factors used in this study are at low resolution, these data are, to the authors' knowledge, of the best quality available. The use of images over a large spatial area (not just focussed over a single field but over several) enabled us to extract ranges of values for each environmental and anthropogenic factor and to consider them in our analysis.

Statistical analysis of the data

All available OTU presence data at each still image location were organized into an OTU presence/absence matrix in which each line of the matrix corresponds to a single still image location and each column record the presence or absence of a specific OTU. Hence, single photographs were chosen as the sampling unit here. Individual sampling units typically had abundances of tens of individuals, which are considered to be sufficient for robust analysis. Environmental and anthropogenic variables were checked for correlations, using the R package corrplot (Wei and Simko, 2017). Hence, depth, slope, salinity, variance of salinity, and variance of temperature were removed from the analysis as these variables showed strong correlation with ruggedness and temperature respectively (see Supplementary Figure S2). The remaining environmental and anthropogenic variables were then organized into an environmental matrix. Finally, a spatial matrix was constructed with the fifteen positive spatial eigenvectors extracted through dbMEM conducted with the R package adespatial (Dray *et al.*, 2018). Owing to the resolution of our dataset, the first eigenvectors created through this analysis will describe large spatial scale changes, in this study over several tens of kilometres (so across fields) while the last eigenvectors will relate to small spatial scale changes across tens of meters (within field).

Stepwise selections of statistically significant spatial, environmental and anthropogenic variables were then conducted through the construction of RDA models. RDA is an extension of PCA in which the response variables (here megafaunal composition) can be modelled as a function of multiple explanatory variables (Zuur *et al.*, 2007). Hellinger standardization was applied on the OTU matrix to reduce the weight of rare OTUs (present in fewer images) and to maintain linear relationships between OTUs and environmental/anthropogenic variables (Legendre and Gallagher, 2001). The stepwise selection process retained five spatial eigenvectors (MEM1, MEM3, MEM4, MEM13, and MEM15), three environmental variables (substrate, temperature, and variance in temperature) and four anthropogenic variables (distance to well and distance to pipeline, intensity of mobile and static demersal fishing) (Table 3).

To examine the impact of spatial and environmental variables on OTUs presence/absence, a total RDA and two partial RDA (a spatial pRDA and an environmental pRDA) models were constructed following Borcard *et al.* (1992). The total RDA model included all the spatial and environmental variables as constraints to the OTUs data. The spatial pRDA model included all spatial variables as constraints to the OTUs data while all environmental variables taken into account within a condition on the model (Borcard *et al.*, 1992). The environmental pRDA model was built as the opposite to the spatial pRDA model (Borcard *et al.*, 1992). The variation of OTUs presence/absence data could then be partitioned, by taking into account the results from all three models, into four components: pure spatial, pure environmental, spatial and environmental, and unexplained (Borcard *et al.*, 1992). Furthermore, the total RDA model biplot was analysed to determine the relationship between the spatial and environmental variables and the environmental pRDA model biplot was drawn to investigate the influence of individual environmental factors on specific OTUs. The 15 OTUs most impacted by the selected environmental variables were also extracted based on their RDA scores. All RDA and pRDA models were conducted with R package vegan (Oksanen et al., 2017). All the statistical analysis steps were conducted in RStudio (RStudio Team, 2015).

Results

General results from the image analysis

Dominant substrate type differed between FSC sites. Gravel/cobble and sand were the most frequent dominant substrate types recorded in this study (Figure 3a). Sand was dominant at Clair, Rosebank, and William whereas gravel/cobble was the most frequent substrate type at Foinven-Schiehallion-Loyal and Laggan. Hard substrate formed by boulders was predominantly recorded at Suilven (Figure 3a). About 92% of the images analysed did not contain any objects (Figure 3b). Pipelines were recorded on 3.1% of the still images while chains and ropes were present on 2.5% of the still images. No anthropogenic objects were detected at the Rosebank, Suilven and William sites. On the contrary, Foinaven-Schiehallion-Loyal appeared to be the most heavily impacted site as 18.8% of images included an anthropogenic object (Figure 3b). Trawl marks were observed on 1.7% of the images analysed (Figure 3c). This proportion reached a maximum of 17.4% at William. No trawl marks were recorded at Rosebank and Suilven (Figure 3c).

Some OTUs included in this study were common across the whole study area. Five OTUs were amongst the most prevalent OTUs in the overall study area as well as at each site: encrusting sponges, cushion sponges, globular sponges, flabellate sponges, and Asteroidea (Figure 4). *Cidaris sp*, Ophiuroidea, and Echinoidea were also often detected in the whole study area and at most sites (Figure 4). However, some OTUs were characterized by a rather site specific distribution. Notably, branching sponges were only often encountered at Foinaven-Schiehallion-Loyal (12.6%, Figure 4). Pycnogonida were amongst the most prevalent OTUs at Rosebank (4.2%) but mainly absent from other sites and soft corals (Alcyonacea 1 and 2) were common at Suilven (Figure 4).

Overview of RDA and pRDAs results

The total RDA and pRDA models constructed in this study allow us to determine the relationships between spatial and environmental variables. All three models were statistically significant (Supplementary Table S1). In total, 15.1% of the OTU presence/absence data was explained by the selected spatial and environmental variables while 84.9% of the variation remained unexplained (Figure 5). Of the 15.1% of variation explained, 8.0% was accounted for by environmental changes whereas 2.6% was explained by spatial variables (Figure 5). The remaining 4.5% of OTUs variation was a product of environmental and spatial variables interactions (Figure 5). When considering the total RDA biplot (Figure 6), it is clear that substrate type, temperature, and demersal fishing (both static and mobile) are the main environmental variables influencing OTUs distribution. MEM1, MEM3, and MEM15 seem to be the main spatial variables affecting the distribution of OTUs in the study area (Figure 6). Relationships between spatial and environmental variables could also be determined. Substrate type, mobile demersal fishing as well as distance to well and pipelines vectors appear related to the vector

Table 2. All OTUs considered in this study organized by class (or phylum for sponges) with short description.

Actinopterygii	
Molva sp.	Dark grey elongated ling
Gaidropsarus argentatus	Elongated lotid fish, red in colour
Macrouridae	Dark grey grenadier
Cottunculus microps	Small grey sculpin
Sebastes sp.	Small red and white rock fish
Lycodes sp.	Brownish elongated fish
Anthozoa	
Actinaria 1	Orange anemone approximately 2 cm wide
Actinaria 2	Small red anemone approximately 1 cm wide
Actinaria 3	Red anemone with elongated tentacles approximately 2 cm wide
Actinaria 4	Dark red/brown anemone approximately 2 cm wide
Ceriantharia	Tube dwelling anemone, white to pale pink in colour
Alcyonacea 1	Pink soft coral
Alcyonacea 2	Dark purple soft coral
Pennatulacea	White/yellow short sea pen
Funiculina sp.	White long sea pen
Scleractinia	Small cup coral approximately 1 cm wide
Zoantharia	Small white polyps found in groups of 10–20 individuals, all about 1.5 cm long
Ascidiacea	
Tunicata	Brown small solitary ascidian with two visible siphons
Asteroidea	
Asteroidea	Sea stars of various colours, often not fully visible (so grouped into one OTU)
Bivalvia	
Bivalvia	Small white/grey bivalve
Bryozoa	
Bryozoa 1	White spiny encrusting bryozoan
Bryozoa 2	Red/brown spiny encrusting bryozoan
Bryozoa 3	White delicate lattice forming bryozoan
Cephalopoda	
Octopoda	Greyish octopus
Decapodiform	Red/orange little squid
Chondrichthyes	
Chimaeriform	Dark grey chimera fish
Batoidea	Dark brown large ray
Clitellata	
Notostomum laeve?	Brown worm-like animal, slightly flattened
Crinoidea	
Crinoidea 1	Large dark brown crinoid
Crinoidea 2	Fine white/pale yellow crinoid
Crinoidea 3	Bright orange large crinoid
Echinoidea	
Cidaris sp.	Beige slate pen sea urchin
Echinoidea	Light red sea urchin
Gastropoda	
Gastropoda	White/grey sea snail
Holothuroidea	
Holothuroidea	Orange to red sea cucumber
Hydrozoa	
Hydrozoa 1	Fine dark stalked hydrozoan with branches perpendicular to the stalk
Hydrozoa 2	Fine dark branching hydrozoa
Hydrozoa 3	Fine white branching hydrozoa
Hydrocoral 1	Short bright white hydrocoral with branches
Hydrocoral 2	Tall hydrocoral with white tentacles and pink egg like structures in its centre
Tubularia sp.	Polyp like animal with pink egg-like structures in its centre emerging from brown tubes
Malacostraca	
Decapoda	Small white and red shrimp
Galatheidae	Small red squat lobster
Brachyura	Orange crab
Anomura	Hermit crab
Munnopsurus sp.	Large pink crustacean with long antennae
Maxillipoda	
Cirripedia	Small white barnacle
Myxini	
Myxini	Light grey/beige hagfish
Ophiuroidea	
Ophiuroidea	Brittle stars of various colours, often not fully visible (so grouped into one OTU)
Gorgonocephalus sp.	Yellow and red basket star
Polychaeta	
Sabellida	Brown tube building worm with white feeding tentacles
Porifera	
Globular Sponges	Bright white round sponge, potentially *Geodia* sp.?
Branching Sponges	Beige delicate branching sponge
Verrucose Sponges	Brown flat sponge with emerging tubular structures, often covered by sediments
Clathrate Sponges	Lattice forming sponge, often white in colour around 3 cm in diameter.
Lobose Sponges	Lobe forming white glass sponge, potentially *Asconema* sp.?
Carnivorous Sponges	Small white stalked sponge with round ended appendices perpendicular to the stalk.
Flabellate Sponges	Fan-shaped sponge, light brown/beige in colour, potentially *Phakelia* sp.?
Cushion Sponges	Flat cushion shaped sponges of various colours
Encrusting Sponges	Flat and fine encrusting sponges of various colours
Pycnogonida	
Pycnogonida	Yellowish delicate sea spider, about 1–2 cm wide

Continued

representing MEM3. Temperature and variance of temperature vectors are tangential with the MEM13 and MEM15 vectors. Finally, the object vectors are tangential with the MEM1 and MEM4 vectors (Figure 6).

Specific impacts of environmental and anthropogenic factors on megafauna in the FSC

Differences in OTU response to environmental variables was observed on the environmental pRDA biplot (Figure 7). Substrate type strongly constrained the presence of sessile megafauna in the FSC (Figure 7). Sponge OTUs, Asteroidea, hydrozoan OTUs, bryozoan OTUs were all associated with coarser substrates (Figure 7). On the other hand, presence of mobile megafauna seemed constrained by anthropogenic variables including demersal fishing (both mobile and static) and the presence of anthropogenic objects. Decapoda, *Cidaris* sp. and, to a lesser extent, Ophiuroidea were detected at locations with high fishing effort. *Sebates* sp. and *Molva* sp. were associated with larger

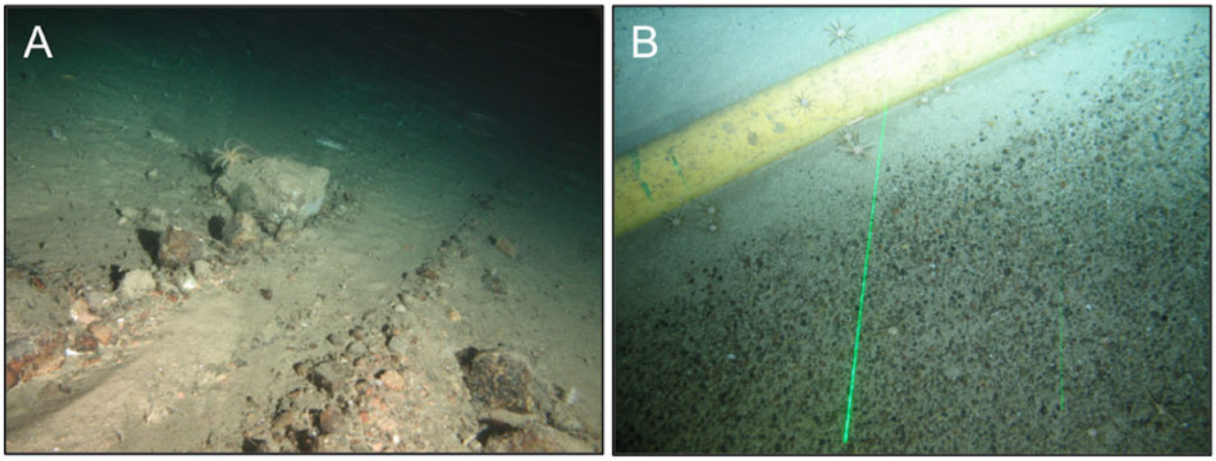

Figure 2. Evidence of anthropogenic activities taking place in the FSC. (a) Trawl marks visible in the seabed. (b) Pipeline as an example of an object detected in this study (lasers separated by 35 cm).

anthropogenic objects such as manifolds and pipelines. Distance to the closest pipeline also affected specific OTUs with Bivalvia being associated with locations furthest away from pipelines (Figure 7).

Discussion

Overall megafauna composition recorded in this study are in accordance with previous studies (Axelsson, 2003; Howell *et al.*, 2007; Jones *et al.*, 2007a; Kazanidis *et al.*, 2019). It has been reported that Cnidaria, Polychaeta, Porifera, Enteropneusta, Mollusca, and Crustacea together represented 90% of the megafauna present in the FSC (Axelsson, 2003). Fish (blackbelly rosefish, *Helicolenus dactylopterus*), squat lobsters, urchins, sea stars, anemones, holothurians, brittle stars as well as sponges were also described as often encountered in the FSC (Howell *et al.*, 2007). Jones *et al.* (2007a) reported high abundances in Annelida and Cnidaria across the Channel with other Phyla including Anthropoda, Echinodermata, and Porifera detected at high density at specific stations. In our study, Porifera (encrusting, cushion, globular, and flabellate sponges), Asteroidea, Echinoidea (*Cidaris* sp. and other Echinoidea), and Ophiuroidea were the most recorded taxonomic groups. Eight sponge morphotypes, similar to the sponges found by Kazanidis *et al.* (2019) were observed in this study, demonstrating the high diversity of sponge morphotypes present in the FSC.

Megafauna community distribution varied across both large and small spatial scales within the FSC. In fact, the eigenvector representing the largest (MEM1) and smallest (MEM15) spatial scales were selected in our model. The selected MEMs did not coincide with the resolution of the environmental variables used, demonstrating that the lower environmental resolution used in this study did not impact the results. Substrate types, distances to wells and pipelines, the presence of objects, and demersal fishing (both static and mobile) appear significant in explaining large spatial scale OTU assembly structures. Conversely, temperature and variance in temperature shaped the OTU community across smaller spatial scales. This is an important finding as it means that the impact of anthropogenic factors in the FSC would not have been detected if considering individual sites (i.e. oil fields). Only by sampling datasets covering several sites, like in this study, can the strong effects of both oil and gas production and fisheries be separated from environmental controls. Our study therefore shows that consideration to spatial scales is important when aiming at understanding how environmental factors and anthropogenic activities impact spatial distribution of species. Several studies have already highlighted the significance of spatial scale in deep-sea marine ecology studies (Henry *et al.*, 2013; Ingels and Vanresuel, 2013; De Leo *et al.*, 2014). However, to the authors' knowledge, no previous work has applied dbMEM analysis to determine the scale of impact of multiple anthropogenic activities on deep-sea benthic communities.

Substrate type and temperature seemed to play a major role in driving benthic megafauna composition. Substrate type along with depth, is known to be an important factor driving deep-sea benthic community composition (Roberts *et al.*, 2008; Howell, 2010; Lacharité and Metaxas, 2017). Substrate type had a stronger impact on sessile fauna, with most sessile OTUs associated with coarser substrate. It is known that most sponges will colonize hard substrate and sponges in the FSC have previously been shown to be associated with coarser substrate types (Kazanidis *et al.*, 2019).

Temperature and variance in temperature also played a role in controlling benthic megafauna spatial distribution. The FSC is characterized by a complex water circulation as five water masses with different salinities, temperatures and nutrient concentrations flow through the channel (Hansen and Østerhus, 2000). The North Atlantic Water and the Modified North Atlantic Water are present in the upper layers of the channel travelling in a northeast direction towards the Arctic Seas while the Modified East Icelandic Water, Norwegian Sea Arctic Intermediate Water, and Norwegian Sea Deep Water are moving below, in a southwest direction towards the North Atlantic (Hansen and Østerhus, 2000). Generally, water temperature on the Shetland side of the FSC can vary from 0°C or lower below 700 m depth to over 10°C above 100 m depth (Berx *et al.*, 2013). Through this complex mixing regime, benthic organisms present in the FSC can therefore be exposed to great changes in temperature of up to 7°C in an hour (Bett, 2001). Ostur sponge grounds as described by Bett (2001) experience, at least occasionally, sub-zero temperatures while the ostur communities described by Klitgaard *et al.* (1997) around

Table 3. Environmental, anthropogenic, and spatial variables considered in this study.

Environmental variables	Anthropogenic variables	Spatial variables
Depth (m)	**Presence of objects**	**MEM1**
Substrate type	Presence of trawl marks	MEM2
Average annual temperature (°C)	**Distance to closest well (m)**	**MEM3**
Variance in annual temperature (°C)	**Distance to closest pipeline (m)**	**MEM4**
Average annual salinity (ppm)	**Static demersal fishing intensity**	MEM5
Variance in annual salinity (ppm)	**Mobile demersal fishing intensity**	MEM6
Neap tide seabed stress (N.m^{-2})		MEM7
Spring tide seabed stress (N.m^{-2})		MEM8
Rugosity		MEM9
Slope (°**)**		MEM10
Eastness		MEM11
Northness		MEM12
		MEM13
		MEM14
		MEM15

Variables selected for the PCA and pRDA models are highlighted in bold.

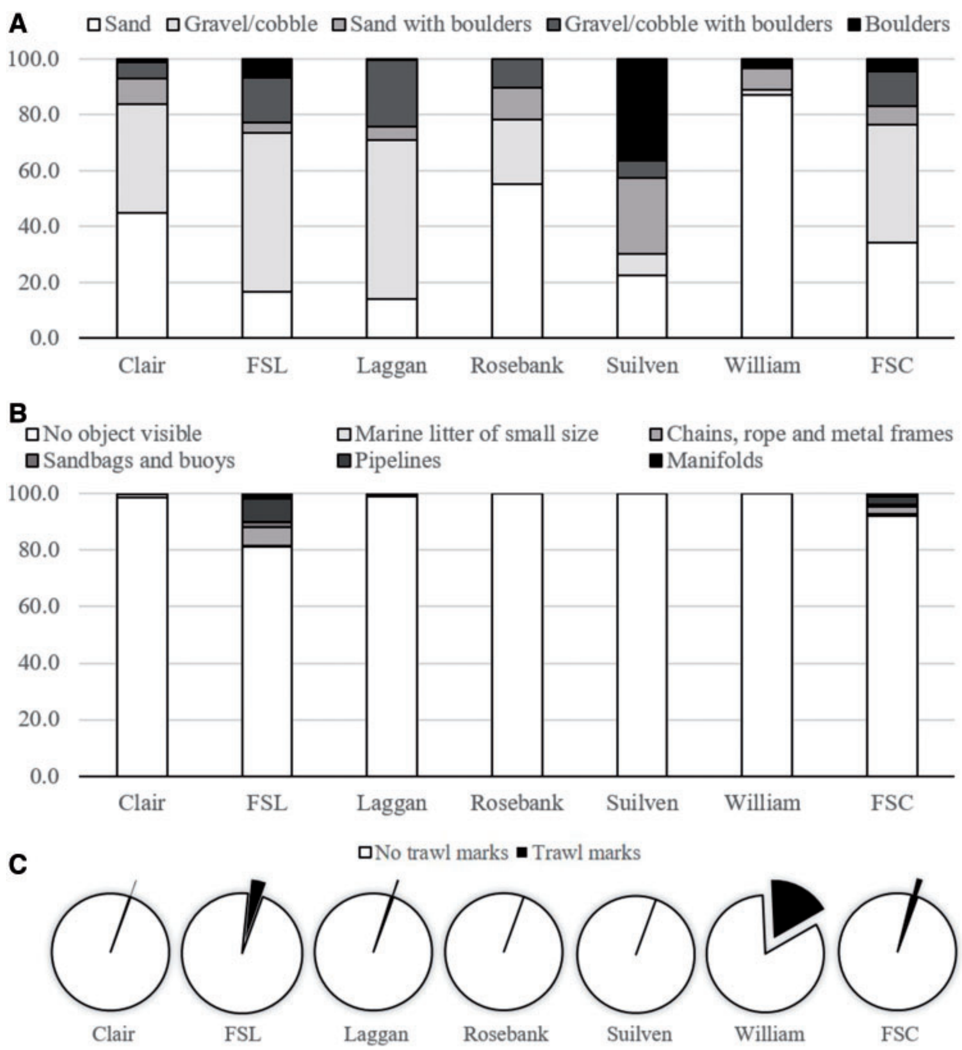

Figure 3. Overall results from image analysis. (a) Proportion of dominant substrate types recorded at each site; (b) proportion of still images with object recorded at each site; (c) proportion of still images with trawl marks recorded at each site. FSL, Foinaven, Schiehallion, Loyal; FSC, Faroe-Shetland Channel.

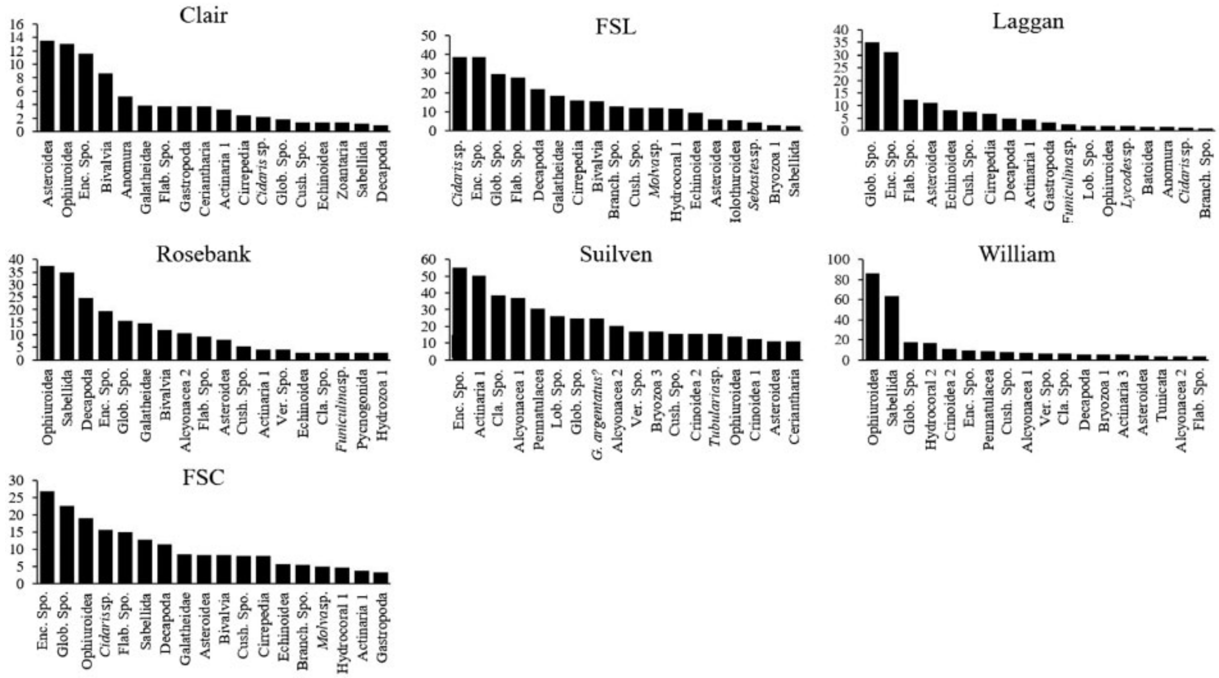

Figure 4. Prevalence of the 18 most frequent OTUs recorded at each site and across all sites combined (FSC). Enc. Spo., for encrusting sponges; Glob. Spo., for globular sponges; Flab. Spo., for flabellate sponges; Cush. Spo., for cushion sponges; Ver. Spo., for verrucose sponges; Branch. Spo., for branching sponges; Lob. Spo., for lobose sponges; Cla. Spo., for clathrate sponges.

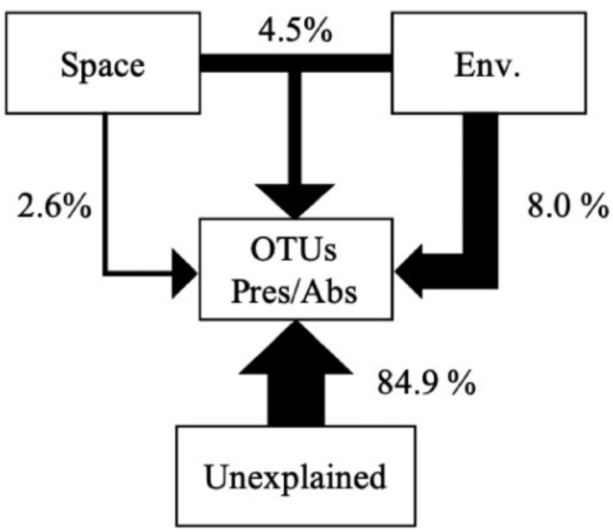

Figure 5. Partition of OTUs presence/absence data variation explained by the pure environmental, pure spatial, spatial, and environmental interactive as well as unexplained components.

the Faroes thrive under water temperatures higher than 5°C. A more recent publication also highlighted the role of temperature and variance in temperature in delimiting the FSC sponge grounds (Davison *et al.*, 2019).

Natural environmental factors were not the only variables detected to exert strong control on the spatial structure of the megafauna. Commercial deep-water fishing is known to have occurred in the FSC (Bett, 2001; Bullough *et al.*, 1998) and both trawl marks as well as fishing gear (ropes) were detected in this study. Both dermersal mobile and static fishing variables were retained in our analysis. Mobile scavenger OTUs (*Cidaris sp*, Decapoda, and Ophiuroidea) were detected in locations where fishing was the strongest whereas sessile OTUs (sponge OTUs, Cirripedia, and Hydrocorals) were associated with areas characterized by low fishing activities. These results confirm the findings of Kazanidis *et al.* (2019) describing fishing effort as one of the strongest factors driving the distribution of sponges in the FSC and demonstrate, once more, the significant impact of deep-sea fishing (both mobile and sessile) on the megabenthos in the FSC. The current proposed management plan from Marine Scotland for the FSC NCMPA include restriction zones for all demersal gears along south-eastern border of the NCMPA and for mobile demersal gear along the north-western border of the NCMPA with a fishing corridor present between the two areas (Marine Scotland, 2017a, b). Recovery/recolonization by sessile megafauna of the restriction zones will need to be studied in the future to determine the efficiency of the management plan.

In our study, distance to wells and pipelines and presence of objects linked to oil and gas activities were significant factors affecting megafauna spatial composition in the FSC. One sessile OTU (Bivalvia) was found clearly linked to locations furthest away from pipelines. In the FSC, physical disturbance from offshore drilling is known to have led to a decrease in diversity in terms of species richness (Jones *et al.*, 2006, 2007b). Overall megafaunal diversity increased with distance from the disturbance, with sessile benthic taxa being the most affected and displaying high mortality rates (Jones *et al.*, 2006, 2007b). A follow-up study published in 2012 showed that the megafauna had only partially recovered between 3 and 10 years post-drilling (Jones *et al.*, 2012). Furthermore, fish OTUs including economically important *Molva* sp. and *Sebastes* sp., were linked with the presence

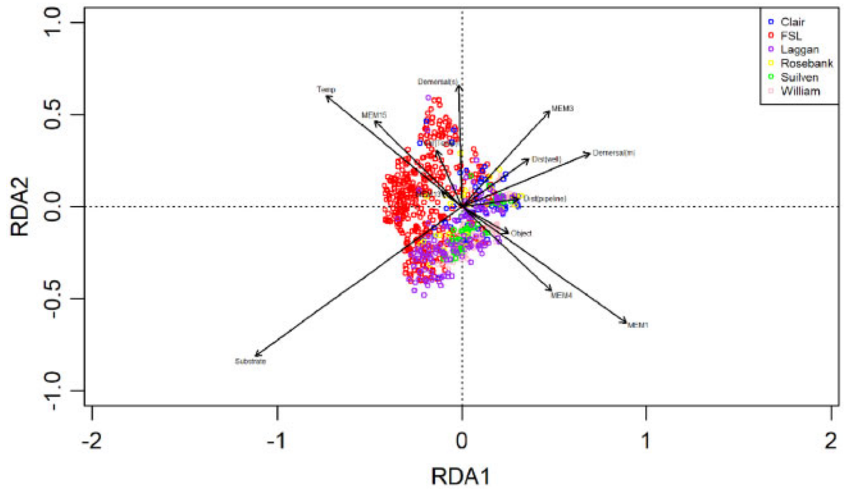

Figure 6. Biplot of total RDA model.

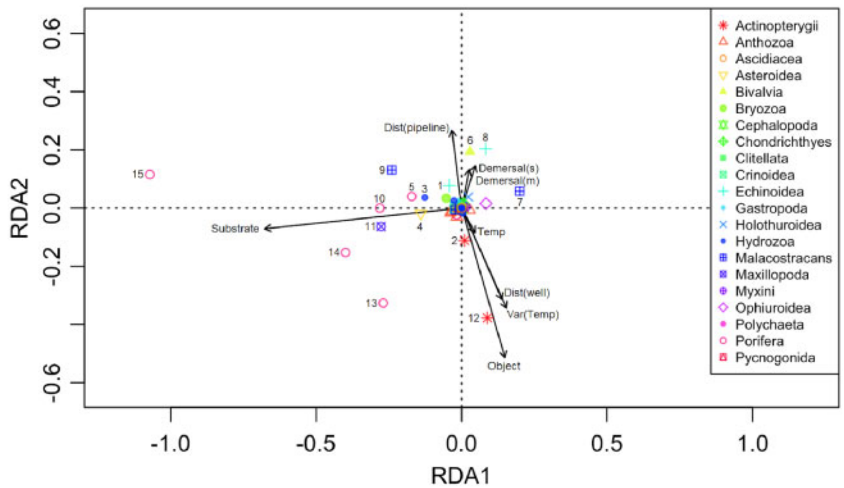

Figure 7. Biplot of pRDA model. For clarity, symbols represent the class/phylum of each OTU (see legend). The 15 most impacted OTUs have also been marked: (1) Echinoidea, (2) *Sebastes* sp., (3) Hydrocoral 2, (4) Asteroidea, (5) Cushion Sponges, (6) Bivalvia, (7) Decapoda, (8) *Cidaris* sp., (9) Galatheidae, (10) Arborescent sponges, (11) Cirripedia, (12) *Molva* sp., (13) Globular Sponges, (14) Flabellate Sponges, and (15) Encrusting Sponges.

of larger oil infrastructure such as pipelines and manifolds. The association of fish species with oil production infrastructures has previously been documented (Seaman *et al.*, 1989). Oil platforms off California can host amongst the most productive fish habitats (Claisse *et al.*, 2014), with productivity values varying greatly from one platform to another (Fowler *et al.*, 2015). Under UK regulation, as offshore infrastructures age, decommissioning options for the physical removal of ageing offshore infrastructure needs to be considered. Physical disturbance is of concern when considering decommissioning as the removal of offshore infrastructure could strongly impact benthic megafauna (Fowler *et al.*, 2014; Vad *et al.*, 2018). Although decommissioning west of Shetland is not yet an immediate issue, consideration around the environmental impact on benthic megafauna of the removal of infrastructures in the MPA will have to be examined.

In conclusion, this study demonstrated the importance spatial scale analysis is to differentiate the impacts of multiple anthropogenic activities from natural environmental variability. Fishing activities in the FSC had significant negative impacts on the sessile megafauna while motile megafauna were found associated with large oil and gas infrastructures. Environmental variables such as temperature and substrate types exerted control over the distribution of the megafauna at small spatial scales. However, both fishing and oil and gas activities were found to structure the megafauna assembly at large spatial scales. As human activities are increasingly taking place in the deep sea, the findings of this study highlight the need for similar large scale analysis to disentangle the complex influences between environmental changes and human impacts on deep-sea ecosystems.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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References

Austin, J. A., Cannon, S. J. C., and Ellis, D. 2014. Hydrocarbon exploration and exploitation West of Shetlands. Geological Society, London, Special Publications, 397: 1–10.

Axelsson, M. B. 2003. The deep seabed environment of the UK continental margin – integration and interpretation of geological and biological data. Doctor of Philosophy, School of Ocean and Earth Science. University of Southampton.

Beaulieu, S. E. 2001. Life on glass houses: sponge stalk communities in the deep sea. Marine Biology, 138: 803–817.

Beazley, L. I., Kenchington, E. L., Murillo, F. J., and Sacau, M. 2013. Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. ICES Journal of Marine Science, 70: 1471–1490.

Beazley, L., Kenchington, E., Yashayaev, I., and Murillo, F. J. 2015. Drivers of epibenthic megafaunal composition in the sponge grounds of the Sackville spur, northwest Atlantic. Deep-Sea Research Part I: Oceanographic Research Papers, 98: 102–114.

Berx, B., Hansen, B., Østerhus, S., Larsen, K. M., Sherwin, T., and Jochumsen, K. 2013. Combining in situ measurements and altimetry to estimate volume, heat and salt transport variability through the Faroe-Shetland Channel. Ocean Science, 9: 639–654.

Bett, B. J. 2001. UK Atlantic margin environmental survey: introduction and overview of bathyal benthic ecology. Continental Shelf Research, 21: 917–956.

Bett, B. J., and Rice, A. L. 1992. The influence of hexactinellid sponge *Pheronema carpenteri* spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic). Ophelia, 36: 217–226.

Borcard, D., Gillet, F., and Legendre, P. 2018 Numerical Ecology with R. Ed. by R Gentleman, K Hornik and G Parmigiani. Springer International Publishing, Cham, Switzerland.

Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling, 153: 51–68.

Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology, 85: 1826–1832.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation'. Ecology, 73: 1045–1055.

Boury-Esnault, N., and Rützler, K. 1997. Thesaurus of Sponge Morphology. Smithsonian Institution Press, Washington D.C.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A. J., Levin, L. A., Priede, I. G., Buhl-Mortensen, P., Gheerardyn, H. *et al.* 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Marine Ecology, 31: 21–50.

Bullough, L. W., Turrell, W. R., Buchan, P., and Priede, I. G. 1998. Commercial deep-water trawling at sub-zero temperatures—observations from the Faroe-Shetland channel. Fisheries Research, 39: 33–41.

Claisse, J. T., Pondella, D. J., Love, M., Zahn, L. A., Williams, C. M., Williams, J. P., Bull, A. S. *et al.* 2014. Oil platforms off California are among the most productive marine fish habitats globally. Proceedings of the National Academy of Sciences of the United States of America, 111: 15462–15467.

Dale, M. R., and Fortin, M. J. 2014. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK.

Davison, J. J., van Haren, H., Hosegood, P., Piechaud, N., and Howell, K. L. 2019. The distribution of deep-sea sponge aggregations (Porifera) in relation to oceanographic processes in the Faroe-Shetland Channel. Deep Sea Research Part I: Oceanographic Research Papers, 146: 55–61.

De Leo, F. C., Vetter, E. W., Smith, C. R., Rowden, A. A., and McGranaghan, M. 2014. Spatial scale-dependent habitat heterogeneity influences submarine canyon macrofaunal abundance and diversity off the Main and Northwest Hawaiian Islands. Deep-Sea Research Part II: Topical Studies in Oceanography, 104: 267–290.

Dray, S., Legendre, P., and Peres-Neto, P. R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196: 483–493.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., *et al.* 2018. adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.1-1. https://CRAN.R-project.org/package=adespatial.

Fowler, A. M., Macreadie, P. I., and Booth, D. J. 2015. Should we "reef" obsolete oil platforms? Proceedings of the National Academy of Sciences of the United States of America, 112: E102.

Fowler, A. M., Macreadie, P. I., Jones, D. O. B., and Booth, D. J. 2014. A multi-criteria decision approach to decommissioning of offshore oil and gas infrastructure. Ocean & Coastal Management, 87: 20–29.

Guihou, K., and Polton, J. A. 2015. Improving understanding of shelf-sea exchange. Ocean Challenge, 21: 26–27.

Guihou, K., Polton, J., Harle, J., Wakelin, S., O'Dea, E., and Holt, J. 2018. Kilometric scale modelling of the north west European shelf seas: exploring the spatial and temporal variability of internal tides. Journal of Geophysical Research: Oceans, 123: 688–707.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F. *et al.* 2008. A global map of human impacts on marine ecosystems. Science, 319: 948–953.

Hansen, B., and Østerhus, S. 2000. North Atlantic-Nordic Seas exchanges. Progress in Oceanography, 45: 109–208.

Henry, L.-A., Moreno Navas, J., and Roberts, J. M. 2013. Multi-scale interactions between local hydrography, seabed topography, and community assembly on cold-water coral reefs. Biogeosciences, 10: 2737–2746.

Hijmans, R. J. geosphere: Spherical Trigonometry. R Package Version 1.5-7. https://CRAN.R-project.org/package=geosphere 20170.

Holt, J., Hughes, S., Hopkins, J., Wakelin, S. L., Penny Holliday, N., Dye, S., González-Pola, C. *et al.* 2012. Multi-decadal variability and trends in the temperature of the northwest European continental shelf: a model-data synthesis. Progress in Oceanography, 106: 96–117.

Howell, K. L. 2010. A benthic classification system to aid in the implementation of marine protected area networks in the deep/high seas of the NE Atlantic. Biological Conservation, 143: 1041–1056.

Howell, K. L., Davies, J. S., Hughes, D. J., and Narayanaswamy, B. E. 2007. Strategic environmental assessment/special area for conservation photographic analysis report. Strategic Environmental Assessment Report, 1–82.

Ingels, J., and Vanreusel, A. 2013. The importance of different spatial scales in determining structural and functional characteristics of deep-sea infauna communities. Biogeosciences, 10: 4547–4563.

Jones, D. O. B., Bett, B. J., and Tyler, P. A. 2007a. Megabenthic ecology of the deep Faroe-Shetland channel: a photographic study. Deep-Sea Research Part I: Oceanographic Research Papers, 54: 1111–1128.

Jones, D. O. B., Gates, A. R., and Lausen, B. 2012. Recovery of deep-water megafaunal assemblages from hydrocarbon drilling disturbance in the Faroe-Shetland Channel. Marine Ecology Progress Series, 461: 71–82.

Jones, D. O. B., Hudson, I. R., and Bett, B. J. 2006. Effects of physical disturbance on the cold-water megafaunal communities of the Faroe-Shetland Channel. Marine Ecology Progress Series, 319: 43–54.

Jones, D. O. B., Wigham, B. D., Hudson, I. R., and Bett, B. J. 2007b. Anthropogenic disturbance of deep-sea megabenthic assemblages: a study with remotely operated vehicles in the Faroe-Shetland Channel, NE Atlantic. Marine Biology, 151: 1731–1741.

Kazanidis, G., Henry, L.-A., Roberts, J. M., and Witte, U. F. M. 2016. Biodiversity of *Spongosorites coralliophaga* (Stephens, 1915) on coral rubble at two contrasting cold-water coral reef settings. Coral Reefs, 35: 193–208.

Kazanidis, G., Vad, J., Henry, L.-A., Neat, F., Berx, B., Georgoulas, K., and Roberts, J. M. 2019. Distribution of deep-sea sponge aggregations in an area of multisectoral activities and changing oceanic conditions. Frontiers in Marine Science, 6: Article 163.

Kenchington, E., Power, D., and Koen-Alonso, M. 2013. Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. Marine Ecology Progress Series, 477: 217–230.

Klitgaard, A. B., and Tendal, O. S. 2004. Distribution and species composition of mass occurrences of large-sized sponges in the Northeast Atlantic. Progress in Oceanography, 61: 57–98.

Klitgaard, A. B., Tendal, O. S., and Westerberg, H. 1997. Mass occurrences of large sponges (Porifera) in Faroe Island (NE Atlantic) shelf and slope areas: characteristics, distribution and possible causes. In Proceedings of the 30th European Marine Biological Symposium, Southampton, UK, 5, pp. 129–142.

Lacharité, M., and Metaxas, A. 2017. Hard substrate in the deep ocean: how sediment features influence epibenthic megafauna on the eastern Canadian margin. Deep Sea Research Part I: Oceanographic Research Papers, 126: 50–61.

Laguionie-Marchais, C., Kuhnz, L. A., Huffard, C. L., Ruhl, H. A., and Smith, K. L. 2015. Spatial and temporal variation in sponge spicule patches at Station M, northeast Pacific. Marine Biology, 162: 617–624.

Legendre, P. D., and Gallagher, E. D. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia, 129: 271–280.

Maldonado, M., Aguilar, R., Bannister, R. J., Bell, J. J., Conway, K. W., Dayton, P. K., Díaz, C., *et al.* 2017. Sponge grounds as key marine habitats: a synthetic review of types, structure, functional roles and conservation concerns. *In* Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, 145–183. Ed. by S. Rossi, L. Bramanti, A. Gori, and C. Orejas. Springer International Publishing Switzerland, Cham, Switzerland.

Marine Scotland 2017a. Northern North Sea Proposal—Measures Only. http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/SACmanagement/Offshore2017.

Marine Scotland 2017b. Northern North Sea Audit. http://www.gov.scot/Topics/marine/marine-environment/mpanetwork/SACmanagement/Offshore2017.

Marliave, J. B., Conway, K. W., Gibbs, D. M., Lamb, A., and Gibbs, C. 2009. Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. Marine Biology, 156: 2247–2254.

Nogués-Bravo, D., Araújo, M. B., Romdal, T., and Rahbek, C. 2008. Scale effects and human impact on the elevational species richness gradients. Nature, 453: 216–219.

Oksanen, J. F., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., *et al.* 2017. vegan: Community Ecology Package. R package version 2.4-5. https://CRAN.R-project.org/package=vegan.

Okutani, T., and Sasaki, T. 2007. Eggs of *Rossia mollicella* (Cephalopoda: sepiolidae) deposited in a deep-sea sponge. Journal of Molluscan Studies, 73: 287–289.

QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org (last accessed 27 September 2019).

Rees, H. R., and Parke, J. 2013. SPE166579. Reservoir Management-Preparing for Field Redevelopment and Restart. *In* SPE Offshore Europe Conference and Exhibition, OE 2013; Aberdeen; United Kingdom; 3 September 2013 through 6 September 2013; Code 101309.

Roberts, J. M., Harvey, S. M., Lamont, P. A., Gage, J. D., and Humphery, J. D. 2000. Seabed photography, environmental assessment and evidence for deep-water trawling on the continental margin west of the Hebrides. Hydrobiologia, 441: 173–183.

Roberts, J. M., Henry, L.-A., Long, D., and Hartley, J. P. 2008. Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic. Facies, 54: 297–316.

RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. http://www.rstudio.com/.

Seaman, W. J., Lindberg, W. J., Gilbert, C. R., and Frazer, T. K. 1989. Fish habitat provided by obsolete petroleum platforms off Southern Florida. Bulletin of Marine Science, 44: 1014–1022.

Vad, J., Kazanidis, G., Henry, L.-A., Jones, D. O. B., Tendal, O. S., Christiansen, S., Henry, T. B., *et al.* 2018. Potential impacts of offshore oil and gas activities on deep-sea sponges and the habitats they form. Advances in Marine Biology, 58: 06Z.

Wei, T., and Simko, V. 2017. R package "corrplot": Visualization of a Correlation Matrix (Version 0.84). https://github.com/taiyun/corrplot.

Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology, 30: 377–392.

Wiens, J. 1989. Spatial Scaling in Ecology. Functional Ecology, 3: 385–397.

Zuur, A., Ieno, E. N., and Smith, G. M. 2007. Analyzing Ecological Data. Springer Science & Business Media, New York, NY.

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